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1.—The Environment of the Quokka *(Setonix brachyurus)* in the Darling Range, Western Australia

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The more constant environment of the mainland quokkas and their maintenance of good condition through the summer are contrasted with the seasonal extremes and loss of condition on Rottnest.

Introduction

Owing to summer drought and the low capacity of the sandy soil for retaining water, most Rottnest plants grow only in winter and spring. They consequently contain much less water and protein in March and April than in August and September (Storr 1961). As their food deteriorates, so the quokkas rapidly lose weight, and their fur becomes increasingly frowsy and verminous. In contrast, a small series of quokkas from the Darling Range north of Jarrahdale showed no significant seasonal variation in condition (Sadleir 1959). It therefore became important to study the environment of these quokkas, if only for a better understanding of the defects of Rottnest.

Habitat

At Jarrahdale (and apparently everywhere on the mainland) quokkas live in densely vegetated swamps. Some water is always present, whereas on Rottnest it is restricted in summer to a few small seepages round the salt lakes and the coast. Aggravating the prevailing absence of fresh water on Rottnest is the scarcity of good shade. On hot days the temperature in a typical quokka shelter on Rottnest exceeded official shade temperatures by 9-22°F, whereas at Jarrahdale it was 5-12° lower than official readings (Sadleir 1959).

The lower than shade temperature at ground level in Jarrahdale swamps is due to the great depth and stratification of the plant cover. The lowest story consists of tall sedges, *Cladium procissii* and *Lepidosperma tetraquetrum,* interspersed with shrubs of *Acacia divergens, A. alata, Oxylobium lincarifolium, Mirbelia dilatata, Bossiaea biloba, Aotus cordifolia,* and *Boronia clatior.* Next is a layer of tall shrubs, mostly *Agonis linearifolia,* whose canopy is usually closed, and through which emerge scattered small trees; *Melaleuca parviflora, Banksia littoralis,* and *Albizzia distachya.* Above all these are the tall eucalypts, *E. patens* and *E. calophylla.*

Quokka runways (more appropriately, tunnels) intersect the sedge zone, and it is here that the animals hide up during the day. At night they come out to feed not only in the swamp itself but also along its edges, where the ground cover is much lower and more open. The vegetation of these marginal flats consists principally of small sedges, *Cladium laxum, Tetrariopsis octandra, Cyathochaete avenacea,* and *Lomandra endlicheri;* perennial herbs, *Thomasia foliosa, T. pauciflora,* and *Trachymene compressa*; and the fern *Pteridium aquilinum.* As the land rises the ground cover quickly merges with the highly sclerophyllous undershrubbery of the jarrah forest.

The vegetation of the swamps and their margins is thus dominated by sedges, perennial herbs, and leguminous and myrtaceous shrubs. In contrast to Rottnest, succulents, i.e. Chenopodiaccae, Aizoaceae etc., are completely absent. Grass is rare and represented by a single species (*Tetrarrhena laevis*). Indigenous annual herbs are an insignificant element in the flora, and no alien species have become established where the vegetation remains undisturbed.

Seasonal variation in nutrients

The terminal foliage of plants growing in and beside a quokka swamp near the source of Manjedal Brook (3 miles north of Jarrahdale) were analysed for water and protein on various occasions in 1958-9. The results are set out in Table 1, an asterisk prefixing species known to be eaten by quokkas (these were found by searching the vegetation along runways for evidence of browsing).

Almost all the shrubs and herbs growing on the dry lateritic soil above the swamp have a winter growth regime. Fragmentary data (not tabulated) indicate that water and protein levels, as on Rottnest, are considerably higher in spring than autumn.

Plants growing on the clayey soil of the marginal flat have generally a similar regime; though there is no great contrast between spring and autumn values of water and protein. *Pteridium* alone of the seven species has summer rather than winter growth, without, however, marked seasonal variation in nutrients.

Of the eleven species growing in water or permanently damp soil, only two, *Aotus* and *Oxylobium,* have a winter growth regime; but again seasonal fluctuation in nutrients is quite small. Four species, *Acacia alata, Albizzia, Eucalyptus patens,* and *Mirbelia,* have a summer growing season; while the remainder, including the two sedges, scarcely change in protein and water content.

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TABLE 1

Crude protein content (% dry weight), with water content (% wet weight) in brackets, of terminal foliage of common plants at Manjedal Brook. Known food plants are asterisked.

	June and July	October	January	March
Swamp Species—				
Acacia alata	10·6 (54)		11·8 (61)	13·7 (58)
**Agonis linearifolia*	6·9 (58)	8·1 (58)	6·4 (58)	8·4 (59)
Albizzia distachya	15·3 (62)		16·0 (61)	20·4 (65)
**Aotus cordifolia*	9·5 (72)			7·3 (59)
Astartea fascicularis	5·4 (53)	7·0 (56)	4·6 (50)	4·8 (52)
Banksia littoralis	5·7 (53)		5·7 (54)	6·0 (56)
Cladium preissii	4·5 (40)	4·2 (40)	4·0 (43)	4·3 (44)
Eucalyptus patens		6·3 (54)	8·3 (66)	7·8 (65)
**Lepidosperma tetraquetrum*	4·8 (64)	4·7 (61)	5·0 (63)	4·4 (63)
Mirbelia dilatata	8·7 (68)		9·7 (66)	12·2 (73)
**Oxylobium linearifolium*	12·9 (64)		11·6 (59)	12·2 (63)
Marginal Flat Species—				
Bossiaea biloba		8·3 (58)	7·7 (45)	6·8 (38)
**Cladium laxum*	4·8 (60)		4·8 (64)	3·9 (56)
Pteridium aquilinum	6·3 (52)		6·6 (55)	7·0 (52)
Tetrariopsis octandra		4·7 (44)		3·3 (41)
**Tetrarrhena laevis*	9·8 (61)	7·2 (62)	6·7 (53)	6·1 (53)
Thomasia foliosa	6·7 (49)	8·6 (57)	7·6 (59)	4·3 (50)
Thomasia pauciflora	5·9 (49)	8·6 (53)	6·2 (56)	7·2 (54)

At all seasons there are some plants in or beside the swamp putting on fresh growth. Because of this and the small intra-specific fluctuation in nutrients, there will likewise be little seasonal variation in the quokkas' intake of water and protein. To illustrate this constancy the data in Table 1 have been averaged and graphed (Fig. 1). Although these averages are not necessarily the same as those of their actual food, the latter must vary in the same way and indeed cannot be greatly different. For comparison, mean water and protein content of the food of Rottnest quokkas are also graphed (data from Storr 1961).

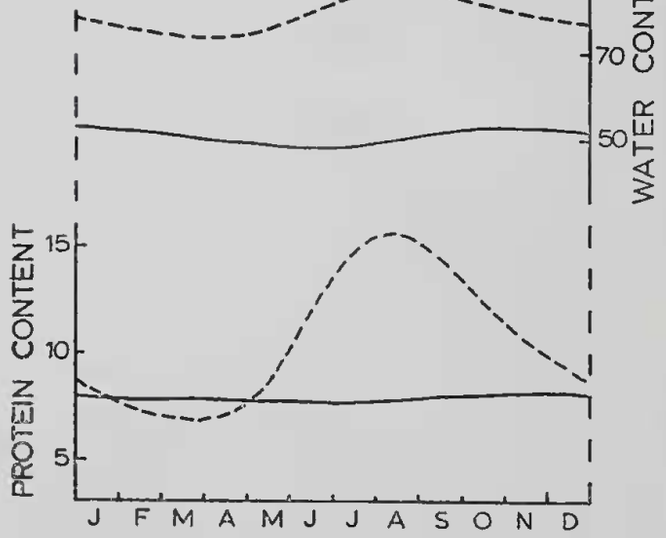

Fig. 1.—Seasonal changes in protein and water content of vegetation. Full lines, plants at Manjedal Swamp; broken lines, food plants of Rottnest quokkas.

Discussion

The absence of marked seasonal fluctuation in the condition of Jarrahdale quokkas is undoubtedly due to their relatively stable plane of nutrition. What is not so easily explained is how they maintain good condition on a diet that can be little richer in protein than that of Rottnest quokkas at its worst. Perhaps their DMI (daily intake of dry matter) is considerably higher than on Rottnest, where it averages 45 g in adult males (Storr 1963), a much lower rate than in captive quokkas eating dry food but supplied with unlimited water (*cf.* Calaby 1958, and Bentley 1960). Since DMI in ruminants falls as the water content of their food exceeds 80% (Dodsworth and Campbell 1952), the intake of Rottnest quokkas could well be depressed by the succulence of their food (75-85% water).

A perusal of the data in Table 1 shows that the mean water content of the food at Jarrahdale cannot be much greater than 60% throughout the year. It is thus possible that a higher DMI more than compensates for the relatively low protein content of the food of Jarrahdale quokkas.

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